



# Effects of desert plant communities on soil enzyme activities and soil organic carbon in the proluvial fan in the eastern foothills of the Helan Mountain in Ningxia, China

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**Abstract:** It is of great significance to study the effects of desert plants on soil enzyme activities and soil organic carbon (SOC) for maintaining the stability of the desert ecosystem. In this study, we studied the responses of soil enzyme activities and SOC fractions (particulate organic carbon (POC) and mineral-associated organic carbon (MAOC)) to five typical desert plant communities (*Convolvulus tragacanthoides*, *Ephedra rhytidosperma*, *Stipa breviflora*, *Stipa tianschanica* var. *gobica*, and *Salsola laricifolia* communities) in the proluvial fan in the eastern foothills of the Helan Mountain in Ningxia Hui Autonomous Region, China. We recorded the plant community information mainly including the plant coverage and herb and shrub species, and obtained the aboveground biomass and plant species diversity through sample surveys in late July 2023. Soil samples were also collected at depths of 0–10 cm (topsoil) and 10–20 cm (subsoil) to determine the soil physicochemical properties and enzyme activities. The results showed that the plant coverage and aboveground biomass of *S. laricifolia* community were significantly higher than those of *C. tragacanthoides*, *S. breviflora*, and *S. tianschanica* var. *gobica* communities ( $P < 0.05$ ). Soil enzyme activities varied among different plant communities. In the topsoil, the enzyme activities of alkaline phosphatase (ALP) and  $\beta$ -1,4-glucosidase ( $\beta$ G) were significantly higher in *E. rhytidosperma* and *S. tianschanica* var. *gobica* communities than in other plant communities ( $P < 0.05$ ). The topsoil had higher POC and MAOC contents than the subsoil. Specifically, the content of POC in the topsoil was 18.17%–42.73% higher than that in the subsoil. The structural equation model (SEM) indicated that plant species diversity, soil pH, and soil water content (SWC) were the main factors influencing POC and MAOC. The soil pH inhibited the formation of POC and promoted the formation of MAOC. Conversely, SWC stimulated POC production and hindered MAOC formation. Our study aimed to gain insight into the effects of desert plant communities on soil enzyme activities and SOC fractions, as well as the drivers of SOC fractions in the proluvial fan in the eastern foothills of the Helan Mountain and other desert ecosystems.

**Keywords:** proluvial fan; desert plant community; soil enzyme activity; particulate organic carbon; mineral-associated organic carbon; Helan Mountain

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## 1 Introduction

Soil is the largest carbon pool in terrestrial ecosystems with a soil organic carbon (SOC) content of approximately 1550 Pg, accounting for 2/3 of the global soil carbon (C) pool (Scharlemann et al., 2014; Lehmann and Kleber, 2015). Soil has a very important role in response to global climate change and the C cycle process, and small changes in soil may significantly affect the C balance in soil (Hicks et al., 2017; Cotrufo et al., 2019). An increasing number of researchers have recommended classifying SOC into two fractions: particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) (Lavalley et al., 2020; Yu et al., 2022). There are differences in the formation, turnover time, and function of SOC fractions (Cotrufo et al., 2019; Sokol et al., 2019b; Lavalley et al., 2020). The POC is dominated by plant macromolecules with higher carbon-to-nitrogen (C:N) ratios and faster turnover rates, whereas MAOC is dominated by microbially derived fraction with lower C:N ratios and slower turnover rates (Lavalley et al., 2020). Cotrufo et al. (2019) reported a significant difference in the POC in European grasslands. MAOC accounts for more than 50% of the total SOC in forest ecosystems, whereas the main source of SOC molecules adsorbed by MAOC is microbial products and their residual material (Sokol et al., 2019b). However, there are not enough research results to support these turnover processes, and how these processes change with ecosystem type is also not clear.

The relationship between plant communities and soil environment has become a popular topic in the field of ecology (Atwood and Hammill, 2018; Hu et al., 2018; Xu et al., 2023). Desert plant communities have important functions, such as windbreak and sand fixation, which maintain ecosystem stability, and are the core building blocks of desert ecosystems (Token et al., 2022). Soil, an important nutrient reservoir and one of the most basic manifestations of human activity, can provide nutrients to desert plants, thus affecting their long-term growth (Li et al., 2018). Plant community diversity can also influence soil multifunctionality (Singh et al., 2018; Yang et al., 2022). Diverse plant communities secrete different types and amounts of root secretions during growth, which can promote the growth and metabolism of soil microorganisms, thereby increasing the rate of SOC input (Chen et al., 2022a). Additionally, different plant species and combinations can provide different types and qualities of SOC fallout and dead roots, which can be degraded by microorganisms and converted into more stable forms of SOC (Sokol et al., 2019a; Wei et al., 2021). Studies have shown that diverse plant communities can promote soil microbial diversity, thereby increasing the stability and long-term storage of SOC (Breulmann et al., 2012; Lange et al., 2015). Plant community diversity can also influence soil physical properties such as soil structure, aeration, and water retention, which can affect the distribution and stability of SOC (Spohn et al., 2023; Xie et al., 2023). For example, diverse plant communities can promote root growth and the formation of soil aggregates, which can increase soil porosity and aeration, thereby improving SOC distribution and stability (Erktan et al., 2016).

Desert plants, as an important vegetable type that affects desert soils in arid and semi-arid areas, have been shown to affect SOC and enzyme activities to different degrees (Chen et al., 2022b), but due to the complexity of landforms in arid and semi-arid areas, the effects of desert plants on soil nutrients and enzyme activities have rarely been reported, especially in the proluvial fan areas. The Helan Mountain, an important ecological security barrier in Northwest China, is an important natural geographic boundary in China, and the proluvial fan is an important basic geomorphological unit in the eastern foothills of the Helan Mountain (Wei et al., 2023). Owing to the rapid development of ecotourism along the Helan Mountain, the continuous expansion of vineyards in the eastern foothills of the Helan Mountain, and the frequent occurrence of seasonal flash floods, the original ecological environment of the desert grassland

in the proluvial fan in the eastern foothills of the Helan Mountain has been disturbed to a large extent, leading to a series of soil environmental problems (Zhang et al., 2022a). Currently, research on soil ecology in the Helan Mountain mainly focuses on the soil physicochemical properties and vegetation at different altitudes (Zhang et al., 2022b; Wei et al., 2023; Zhang et al., 2023). However, there are few reports on the chemical properties of soils in the desert plant communities of the Helan Mountain, especially on the comprehensive study of soil enzyme activities and SOC fractions in the proluvial fan area. Therefore, it is important to study the effects of desert plants on soil enzyme activities and SOC fractions to maintain the stability of desert ecosystems.

In this study, we selected five different desert plant communities from the proluvial fan in the eastern foothills of the Helan Mountain, and studied the effects of plant communities on soil enzyme activities and SOC fractions. We hypothesized that: (1) soil enzyme activities in different desert plant communities are mainly affected by vegetation biomass and soil nutrients, and when soil nutrients cannot meet microbial metabolic activities, enzyme activities will be reduced to adapt to the environment; and (2) SOC fractions are positively correlated with the aboveground biomass of desert plant communities, and plant residual C can be converted into stable SOC under decomposition by microorganisms and stored in the soil C pool. The study results lay a foundation for soil biological restoration and the construction mechanism of desert plant communities, and provide important scientific support for the ecological restoration projects for maintaining the biodiversity and ecological barrier functions of the Helan Mountain.

## 2 Materials and methods

### 2.1 Study area

The study area (38°34'15"–38°49'40"N, 105°55'25"–106°10'16"E) is located in the Helan Mountain, northwest of Ningxia Hui Autonomous Region, China. The Helan Mountain lies in the southwest-northeast direction, with an average altitude of 2000 m. Among them, the topography in the eastern foothills of the Helan Mountain is high in the west and low in the east, which is mainly a proluvial fan formed by the accumulation of alluvium. The sampling altitude was between 1226 and 1506 m. The study area has a continental monsoon climate with drought, little rain, sufficient sunshine, and a large temperature difference between day and night (Chao et al., 2023). The average annual temperature is 8.5°C, the average daily temperature difference is 10.3°C–15.7°C, the annual precipitation is 180–250 mm (of which 60%–80% is concentrated from June to August), and the average annual evaporation is 2000 mm (Zhao et al., 2024).

### 2.2 Experiment design and sampling

In late July 2023, we investigated five desert plant communities: *Convolvulus tragacanthoides*, *Ephedra rhytidosperma*, *Stipa breviflora*, *Stipa tianschanica* var. *gobica*, and *Salsola laricifolia* communities in the proluvial fan in the eastern foothills of Helan Mountain. During the field survey, we randomly selected four 10 m×10 m plots in each plant community for vegetation investigation, and the community name, plant coverage, herb and shrub species (name and number of individuals) were recorded. At the same time, a quadret of 1 m×1 m was randomly set up in each 10 m×10 m plot to obtain aboveground biomass and plant species diversity. After the investigation, the aboveground plants were taken back to the laboratory after cutting and washed with distilled water at 105°C for 0.5 h, then dried at 65°C to constant weight, and the aboveground biomass was obtained. The soil types of each plant community were investigated separately, and we found that the soil types were sierozem, brown calcic soil, and chestnut soil with a coarse texture and gravel content (International Union of Soil Sciences Working Group World Reference Base, 2014). Soil samples in each plant community were collected by removing the dead leaves and O-layer on the surface, adopting a five-point sampling method. We collected the soil at depths of 0–10 cm (topsoil) and 10–20 cm (subsoil) using a soil auger with a diameter of 5 cm, and then thoroughly mixed the soil from the five points, removed stones, roots, and other

debris, brought it back to the laboratory, and passed it through a 2.00 mm sieve. Each soil sample was divided into two parts: one part was used for the determination of soil pH, SOC, total nitrogen (TN), available phosphorus (AP), total phosphorus (TP), available potassium (AK), total potassium (TK), POC, and MAOC, and the other part was stored in a refrigerator at  $-20^{\circ}\text{C}$  for the determination of soil enzyme activities.

## 2.3 Laboratory analyses

### 2.3.1 Soil physicochemical properties and enzyme activities

The soil pH was determined using a PHS-3G pH meter (the soil-to-water ratio was 1.0:2.5) and the SWC (%) was determined using the classical drying method. SOC (g/kg) was determined by the potassium dichromate external heating volume method (Walkley and Black, 1934), and TP and TN contents (g/kg) were determined by molybdenum-antimony anti-colorimetry and Kjeldahl nitrogen determination method, respectively; TK (g/kg) was obtained by flame photometry, AP (g/kg) was determined by  $\text{NaHCO}_3$  extraction method, and AK (g/kg) was extracted by  $\text{NH}_4\text{OAc}$  and flame spectrophotometry.  $\text{NO}_3^-$ -N (mg/kg) and  $\text{NH}_4^+$ -N (mg/kg) in soils were extracted with 0.01 mol/L  $\text{CaCl}_2$  solution, and then the filtrate was determined by flow injection automatic analyzer (FIA-Compact, Braun and L  bbe, Norderstedt, Germany). We extracted and cultured soil extracellular enzymes according to the method described by Zhang et al. (2018). Soil enzyme activities ( $\mu\text{mol}/(\text{d}\cdot\text{g})$ ) of Alkaline phosphatase (ALP),  $\beta$ -1,4-glucosidase ( $\beta\text{G}$ ), Cellobiohydrolase (CBH),  $\beta$ -xylosidase ( $\beta\text{X}$ ), leucine aminopeptidase (LAP),  $\beta$ -1,4-N-acetylglucosaminidase (NAG), and cellulase ( $\beta\text{D}$ ) were measured using 96-well enzyme plate fluorescence analysis (Stone et al., 2014).

### 2.3.2 SOC fractions

Sodium hexametaphosphate was used to separate the two SOC fractions (POC and MAOC) (Bradford et al., 2008; Sokol et al., 2019a). Specifically, 20 g air-dried soil samples were added to the triangle bottle, and 60 mL of 5% sodium hexametaphosphate solution was added to the shaker (BSD-YF2600, Qingdao Mingbo Environmental protection Technology Co., Ltd., Qingdao, China) to shake (180 r/min, 18 h) to disperse the aggregates, and then washed with distilled water through a  $53\ \mu\text{m}$  sieve to separate the POC fraction ( $\geq 53\ \mu\text{m}$ ) and the MAOC fraction ( $< 53\ \mu\text{m}$ ). After drying at  $65^{\circ}\text{C}$  to constant weight, the fractions collected in the beaker were weighed and the separation ratio was obtained. Through a 0.15 mm sieve, the contents of two separated functional SOC fractions (POC and MAOC) were determined by the potassium dichromate-external heating volumetric method.

## 2.4 Calculation of plant species diversity

Based on the field survey data, we calculated the plant species diversity in each plant community using the Shannon-Wiener index, and the formula was as follows (Zhang et al., 2015):

$$W = -\sum_{i=1}^S P_i \ln P_i, \quad (1)$$

where  $W$  is the Shannon-Wiener index;  $S$  is the total number of species; and  $P_i$  is the proportion of the number of individuals of the species  $i$  to the total number of individuals.

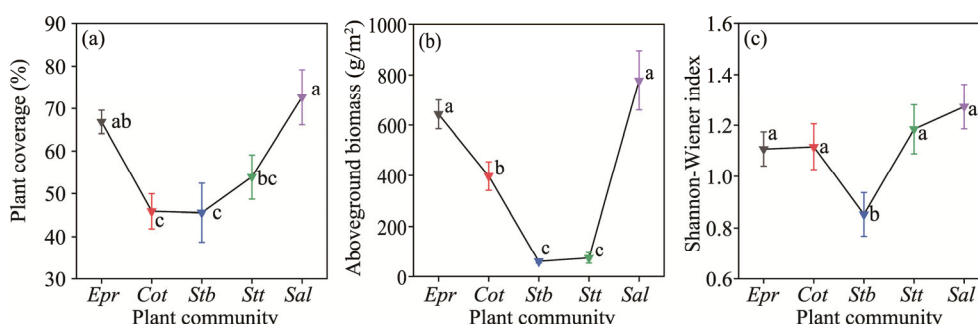
## 2.5 Data analysis

All experimental data were compiled in Microsoft Excel 2013 and checked for homogeneity of variance and normality prior to data analysis. Statistical significance ( $P < 0.05$  or  $P < 0.01$ ) was determined using one-way analysis of variance (ANOVA). Plots were constructed using the OriginPro 2021 software (OriginLab, Massachusetts, USA). Structural equation modeling (SEM) was performed using the lavaan package in R 3.6.0 (R Core Team, 2019). SEM was used to analyze the potential direct and indirect effects of plant characteristics (plant coverage and plant species diversity), and soil characteristics (soil physicochemical properties and enzyme activities) on POC and MAOC. The path coefficients indicated the direction and strength of the direct influence of the two variables. Therefore, we employ a partial least squares path model (PLS-PM) to explain these complex effects on POC and MAOC accumulation.

### 3 Results

#### 3.1 Plant species diversity

Five different plant communities were investigated, and the results showed that plant coverage, aboveground biomass, and Shannon-Wiener index of *S. breviflora* community were significantly lower than those of the other communities (Fig. 1). The plant coverage and aboveground biomass of *S. laricifolia* community were significantly higher than those of *C. tragacanthoides*, *S. breviflora*, and *S. tianschanica* var. *gobica* communities ( $P<0.05$ ), and were higher than those of the other four plant communities by 25.84%–37.31% and 48.87%–92.10%, respectively (Fig. 1a and b). The Shannon-Wiener index of *S. breviflora* community ( $0.85\pm0.08$ ) was significantly lower by 23.06%–33.10% compared to other plant communities (Fig. 1c).



**Fig. 1** Plant coverage (a), aboveground biomass (b), and Shannon-Wiener index (c) of different plant communities. Epr, *Ephedra rhytidosperma*; Cot, *Convolvulus tragacanthoides*; Stb, *Stipa breviflora*; Stt, *Stipa tianschanica* var. *gobica*; Sal, *Salsola laricifolia*. Lowercase letters indicate that the differences are significant in different plant communities ( $P<0.05$ ). Bars are standard errors ( $n=4$ ).

#### 3.2 Soil physicochemical properties and enzyme activities

Our results showed that the soil physicochemical properties differed among the plant communities (Table 1). SWC was significantly higher in *C. tragacanthoides* community than in the other plant communities, and soil pH and AK content were significantly lower in the topsoil of *E. rhytidosperma* community than in the topsoil of the other plant communities ( $P<0.05$ ), whereas soil TP measurements showed an opposite trend. Soil TN content and  $\text{NH}_4^+\text{-N}$  concentration were significantly higher in *S. tianschanica* var. *gobica* community than in the other plant communities ( $P<0.05$ ), and vice versa for  $\text{NO}_3^-\text{-N}$  concentration. In *S. tianschanica* var. *gobica* community, soil TK content was significantly higher ( $P<0.05$ ) than that in the other plant communities.

Soil enzyme activities involved in soil C, nitrogen (N), and phosphorus (P) transformations showed differences in different plant communities (Fig. 2). Among them, ALP,  $\beta\text{G}$ ,  $\beta\text{X}$ , and  $\beta\text{D}$  activities were higher in the topsoil than in the subsoil, and  $\beta\text{G}$  and ALP activities were significantly higher in the topsoil of *E. rhytidosperma* and *S. tianschanica* var. *gobica* communities than in the topsoil of other plant communities ( $P<0.05$ ; Fig. 2a and b). LAP and  $\beta\text{D}$  activities were highest in the soils of *S. laricifolia* community, and NAG activity was highest in the topsoil of *S. laricifolia* community (Fig. 2f).

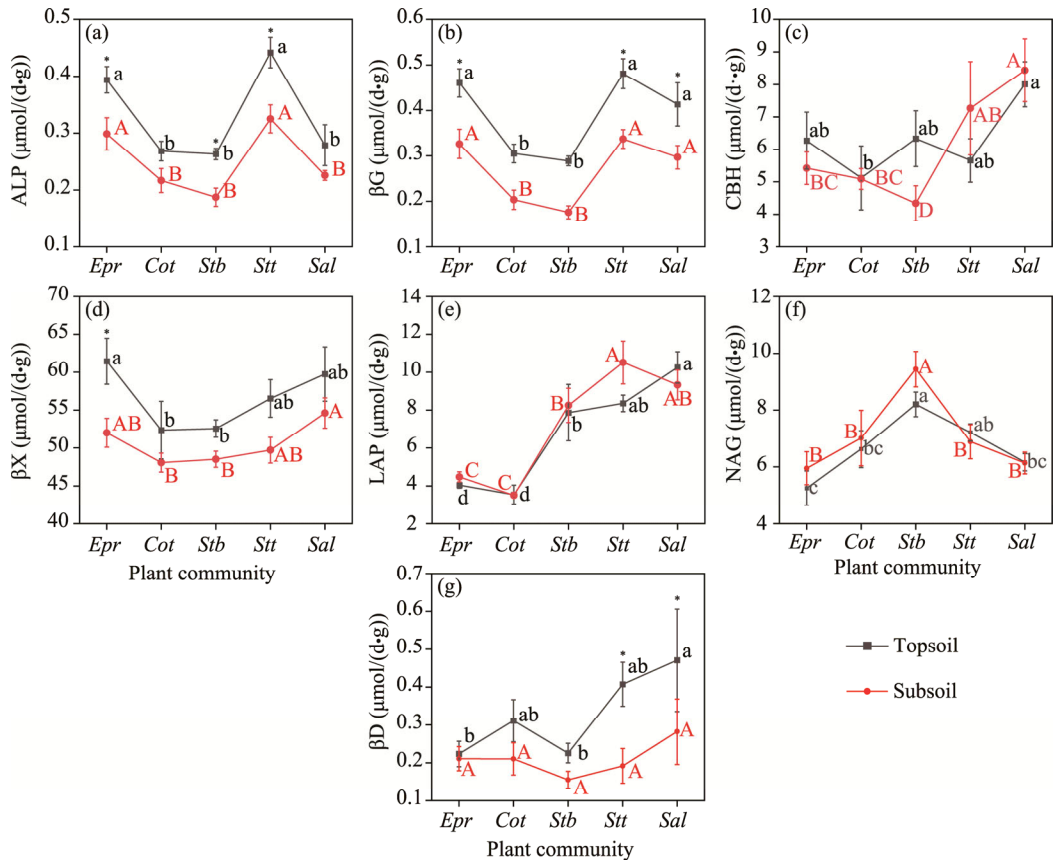
#### 3.3 SOC fractions

POC and MAOC contents were higher in the topsoil than in the subsoil among all plant communities, and the contents of POC in the topsoil were 18.17%–42.73% higher than those in the subsoil among plant communities (Fig. 3a and b). The highest contents were found in *S. breviflora* community in the form of POC ( $4.90\pm0.55$  g/kg), MAOC ( $8.83\pm0.34$  g/kg), and SOC ( $15.31\pm1.20$  g/kg). Compared to other plant communities, the topsoil contained 7.77%–37.27%, 19.37%–58.41%, and 10.68%–36.22% more POC, MAOC, and SOC than the subsoil in *S. breviflora* community, respectively. *C. tragacanthoides* community had the lowest SOC content (topsoil:  $9.76\pm0.49$  g/kg; subsoil:  $11.22\pm0.76$  g/kg), which was significantly lower than the other plant communities ( $P<0.05$ ; Fig. 3c).

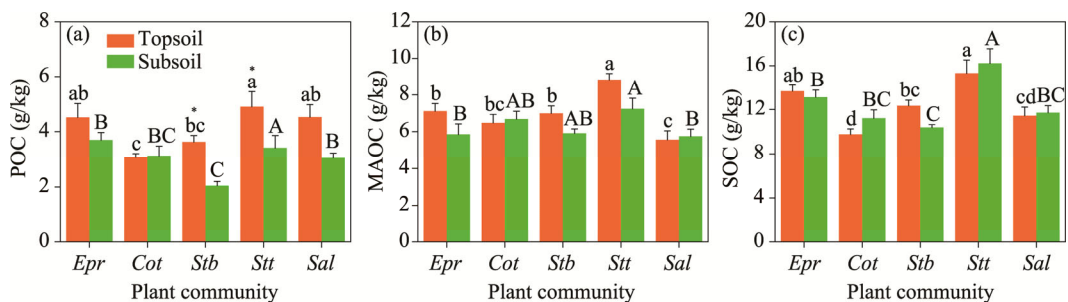
Table 1 Soil physicochemical properties of the topsoil and subsoil in different plant communities

Plant community	Soi layer	Soil property								
		SWC (%)	pH	TN (g/kg)	TP (g/kg)	TK (g/kg)	AP (mg/kg)	AK (mg/kg)	NH <sub>4</sub> <sup>+</sup> -N (mg/kg)	NO <sub>3</sub> <sup>-</sup> -N (mg/kg)
<i>Ephedra rhytidosperma</i>	Topsoil	0.31±0.03 <sup>b</sup>	7.97±0.05 <sup>b</sup>	1.48±0.06 <sup>b</sup>	0.76±0.06 <sup>a</sup>	7.13±0.29 <sup>c</sup>	24.90±4.25 <sup>ab</sup>	185.52±11.51 <sup>b</sup>	2.73±0.29 <sup>a</sup>	18.47±2.01 <sup>a</sup>
	Subsoil	0.68±0.12 <sup>c</sup>	8.07±0.05 <sup>b</sup>	1.50±0.09 <sup>b</sup>	0.76±0.07 <sup>a</sup>	7.15±0.18 <sup>c</sup>	23.84±3.55 <sup>ab</sup>	115.90±12.00 <sup>b</sup>	2.16±0.26 <sup>a</sup>	20.89±2.84 <sup>ab</sup>
<i>Convolvulus tragacanthoides</i>	Topsoil	1.96±0.59 <sup>a</sup>	8.12±0.03 <sup>a</sup>	1.16±0.06 <sup>c</sup>	0.58±0.02 <sup>b</sup>	8.18±0.46 <sup>ab</sup>	19.00±1.75 <sup>b</sup>	277.09±13.20 <sup>a</sup>	1.99±0.10 <sup>b</sup>	15.85±2.20 <sup>a</sup>
	Subsoil	3.33±0.19 <sup>a</sup>	8.11±0.03 <sup>b</sup>	1.39±0.09 <sup>bc</sup>	0.72±0.11 <sup>ab</sup>	8.65±0.42 <sup>b</sup>	31.40±5.55 <sup>a</sup>	228.82±15.48 <sup>a</sup>	1.91±0.16 <sup>a</sup>	25.71±3.02 <sup>a</sup>
<i>Stipa breviflora</i>	Topsoil	0.84±0.09 <sup>b</sup>	8.21±0.02 <sup>a</sup>	1.31±0.04 <sup>ab</sup>	0.58±0.02 <sup>b</sup>	8.27±0.44 <sup>a</sup>	16.13±2.15 <sup>b</sup>	261.98±12.85 <sup>a</sup>	2.00±0.20 <sup>b</sup>	15.85±2.20 <sup>a</sup>
	Subsoil	2.56±0.27 <sup>b</sup>	8.23±0.03 <sup>a</sup>	1.18±0.02 <sup>c</sup>	0.66±0.08 <sup>ab</sup>	9.61±0.44 <sup>a</sup>	20.18±3.48 <sup>ab</sup>	247.89±8.97 <sup>a</sup>	2.07±0.18 <sup>a</sup>	25.71±3.02 <sup>a</sup>
<i>Stipa tianschanica</i> var. <i>gobica</i>	Topsoil	0.67±0.13 <sup>b</sup>	8.13±0.04 <sup>a</sup>	1.86±0.14 <sup>a</sup>	0.55±0.01 <sup>b</sup>	9.04±0.21 <sup>a</sup>	23.06±3.33 <sup>ab</sup>	287.49±18.19 <sup>a</sup>	3.15±0.19 <sup>a</sup>	9.14±0.54 <sup>b</sup>
	Subsoil	0.89±0.19 <sup>c</sup>	8.05±0.02 <sup>b</sup>	1.95±0.15 <sup>a</sup>	0.55±0.02 <sup>b</sup>	8.29±0.23 <sup>b</sup>	28.93±3.77 <sup>ab</sup>	213.55±30.88 <sup>a</sup>	1.92±0.09 <sup>a</sup>	8.11±1.46 <sup>d</sup>
<i>Salsola laricifolia</i>	Topsoil	0.35±0.05 <sup>b</sup>	8.22±0.03 <sup>a</sup>	1.20±0.09 <sup>c</sup>	0.62±0.02 <sup>b</sup>	7.17±0.36 <sup>bc</sup>	33.02±5.03 <sup>a</sup>	316.70±43.54 <sup>a</sup>	2.49±0.32 <sup>ab</sup>	16.39±2.62 <sup>a</sup>
	Subsoil	0.46±0.06 <sup>c</sup>	8.16±0.04 <sup>ab</sup>	1.28±0.09 <sup>bc</sup>	0.67±0.05 <sup>ab</sup>	7.11±0.24 <sup>c</sup>	18.36±2.08 <sup>b</sup>	189.26±27.24 <sup>a</sup>	1.97±0.12 <sup>a</sup>	12.86±2.02 <sup>cd</sup>

Note: All values in the table are mean±SD. Lowercase letters indicate significant differences between different plant communities in the same soil layer (*P*<0.05).



**Fig. 2** Soil enzyme activities of ALP (a),  $\beta\text{G}$  (b), CBH (c),  $\beta\text{X}$  (d), LAP (e), NAG (f), and  $\beta\text{D}$  (g) in the topsoil (soil depth of 0–10 cm) and subsoil (soil depth of 10–20 cm) of different plant communities. ALP, alkaline phosphatase;  $\beta\text{G}$ ,  $\beta$ -1,4-glucosidase; CBH, Cellobiohydrolase;  $\beta\text{X}$ ,  $\beta$ -1,4-xylosidase; LAP, leucine aminopeptidase; NAG,  $\beta$ -1,4-N-acetylglucosaminidase;  $\beta\text{D}$ , cellulase. Lowercase letters indicate that the differences are significant ( $P < 0.05$ ) in the topsoil; uppercase letters indicate that the differences are significant ( $P < 0.05$ ) in the subsoil. \* indicates that the differences are significant ( $P < 0.05$ ) among different soil layers. Bars are standard errors ( $n=4$ ).



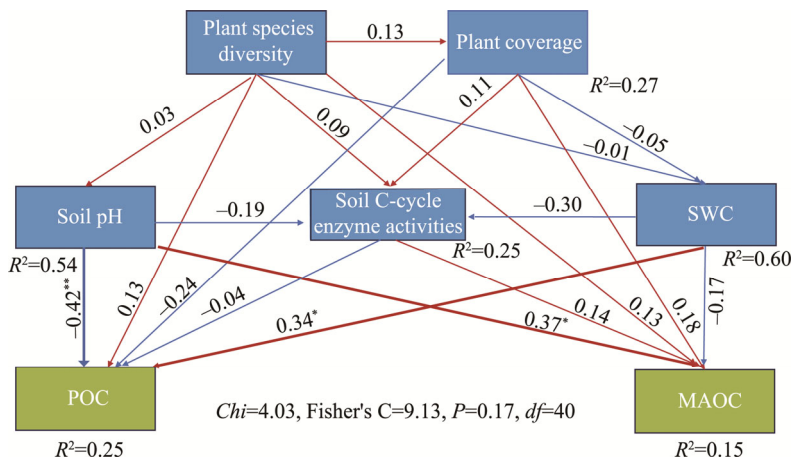
**Fig. 3** Contents of POC (a), MAOC (b), and SOC (c) in the topsoil and subsoil of different plant communities. POC, particulate organic carbon; MAOC, mineral-associated organic carbon; SOC, soil organic carbon. Lowercase letters indicate that soil POC, MAOC, and SOC contents differ significantly ( $P < 0.05$ ) in the topsoil; uppercase letters indicate that soil POC, MAOC, and SOC contents differ significantly ( $P < 0.05$ ) in the subsoil. \* indicates that the differences are significant ( $P < 0.05$ ) among different soil layers. Bars are standard errors ( $n=4$ ).

### 3.4 Influencing factors of POC and MAOC

Factors affecting the two functional SOC fractions (POC and MAOC) were combined to study their effects on POC and MAOC (Fig. 4). According to the SEM, the main factors affecting POC and MAOC included plant species diversity, plant coverage, soil pH, SWC, and soil enzyme activities related to soil organic carbon cycling. Soil pH and SWC had opposite effects on the



formation of POC and MAOC, pH inhibited the formation of POC and promoted the formation of MAOC, whereas SWC had the opposite effect ( $P<0.05$ ).



**Fig. 4** Partial least squares path model (PLS-PM) results of the effects of plant species diversity, plant coverage, soil pH, soil water content (SWC), and soil C-cycle enzyme activities related to SOC cycling on POC and MAOC under different plant communities. The numbers on the arrows indicate the path coefficients. \*,  $P<0.05$ ; \*\*,  $P<0.01$ . Red arrows represent positive correlations, blue arrows represent negative correlations, and the wider arrows represent significant differences ( $P<0.05$ ).  $R^2$  refers to the proportion of variance explained in the assessment of model fit, and the closer it is to 1.00, the more the model explains the variability of the dependent variable, which indicates that the model fit is better.  $df$ , degree of freedom.

## 4 Discussion

### 4.1 Effects of desert plant communities on soil enzyme activities

Related studies have shown that soil enzyme activities reflect changes in soil physicochemical properties and are involved in soil biochemical processes (Li et al., 2020a; Sheng et al., 2020; Wen et al., 2023). Our results showed that ALP and  $\beta$ G activities were significantly higher in *E. rhytidosperra* community than in the other plant communities, which may be due to the strong soil and water conservation capacity of *E. rhytidosperra* in the proluvial fan for its well-developed primary root. During vegetation restoration, the species diversity of plant communities is closely related to the soil enzyme activities (Xiao et al., 2020; Xu et al., 2021). Plant species diversity promotes the community structure and abundance of microorganisms in the soil, which in turn affects the production of microbial metabolites and related proteins (Zhang et al., 2018). In contrast, plant communities influence the nutrients that enter the soil and regulate soil enzyme activities by affecting the soil physicochemical properties (Deng et al., 2019; Li et al., 2020b). However, in areas affected by soil erosion, the action of soil erosion (raindrop splash and surface runoff) leads to the loss of nutrients from topsoil and a decrease of soil enzyme activities (Wang et al., 2011; Costantini et al., 2018; Du et al., 2021).

In this study, we founded that soil  $\beta$ X activities of the four plant communities, except for *C. tragacanthoides* community, decreased with the depth of the soil layer. This may be related to the process of soil formation and development in the proluvial fan in the eastern foothills of the Helan Mountain. With the deepening of the soil layer, the nutrient and aeration conditions of the soil decreased, which in turn inhibited the metabolic capacity of the microbial community, making the enzyme activities of the subsoil significantly lower than those of the topsoil.  $\beta$ X promotes the oxidation of the organic substances in the soil (e.g., phenols, amines, etc.) to produce quinone, which is essential for the development of microbial communities (Liu and Zhang, 2019; Zhang et al., 2022a; Yang et al., 2023). Changes in soil enzyme activities are regulated by many factors, such as climate, soil, and plant age (Cao et al., 2021; Jin et al., 2022). The study area has been significantly disturbed by human activities in the past, and the development of industries such as



grape cultivation is likely to be an important factor in the instability of soil enzyme activities. In addition, owing to the differences in soil nutrients and soil matrices in different plant communities, the extracellular enzyme activities in the soil are different (Cui et al., 2021). Among them,  $\beta$ G and CBH activities played an important role in the SOC cycle, mainly involved in the degradation of cellulose (Fan et al., 2021). High CBH activity was found in *S. laricifolia* community, which may be related to soil nutrients ( $\text{NO}_3^-$ -N and  $\text{NH}_4^+$ -N) and pH. Li et al. (2020a) showed that soil N forms and pH simultaneously affected enzyme activities.

## 4.2 Effects of desert plant communities on POC and MAOC

The results showed that except for *C. tragacanthoides* community, the two SOC fractions in the other plant communities were consistent: the POC and MAOC contents in the topsoil were significantly higher than those in the subsoil (Fig. 3a and b). This is mainly because surface litter preferentially enters the topsoil, and part of it is transformed into SOC and stored in the soil under decomposition by microorganisms (Almeida et al., 2021; Ridgeway et al., 2022; Bourget et al., 2023). The decomposition of exogenous SOC by microorganisms is limited by the lack of nutrients available to soil microorganisms in the subsoil (Liu et al., 2023). As the main product of plant-derived C formation, POC is mainly produced by the decomposition of plant components into microorganisms in the soil (e.g., lignin phenol) (Jia et al., 2021; Hansen et al., 2024). MAOC is mainly produced from microbial-derived C (Sokol and Bradford, 2019; Yu et al., 2022). Microorganisms not only participate in the production of SOC as decomposers, but also participate in the production of SOC through the synergistic action of "ex vivo modification" and "in vivo turnover" through microbial C pump (Liang et al., 2017; Zhu et al., 2020). It has been shown that the contribution of microbial necromass C to SOC is 35%–51% (Wang et al., 2021), and microbial residue C is the main source in the process of MAOC formation (Sokol and Bradford, 2019; Guo et al., 2022; Zhao et al., 2023).

Consistent with our second hypothesis, our results showed that the plant species diversity promoted the production of POC and MAOC in the soil (Fig. 4). Plant species diversity affects SOC accumulation by stimulating the formation of SOC during vegetation restoration and increasing exogenous C in the soil during decomposition by microorganisms (Wang et al., 2022; Spohn et al., 2023). The results showed that the Shannon-Wiener index of *S. breviflora* community was significantly lower than that of *S. laricifolia* community, while the contents of POC, MAOC, and SOC in *S. breviflora* community were higher in the topsoil than in the subsoil (Figs. 1 and 3). After the litter is imported into the soil, it will consume the N source in the soil, which reduces the C:N ratio in the soil (Cheng et al., 2023). Plants with low C:N ratios can rapidly decompose to form POC after entering the soil, whereas plant sources with high C:N ratios cannot be rapidly decomposed and utilized because of the presence of macromolecules that are difficult to rapidly utilize, resulting in low levels of POC, MAOC, and SOC in *S. laricifolia* community (Wei et al., 2021; Ridgeway et al., 2022). Furthermore, with changes in plant species diversity, the source of SOC in the soil is enriched, and the formation of POC and MAOC in the soil is promoted (Hu et al., 2023). SWC indirectly affects the formation and accumulation of SOC by influencing the composition of soil microbial communities (Zhang et al., 2020; Deng et al., 2023; Liu et al., 2023). Owing to the limitations of SWC and aeration in the subsoil, the microbial community activity and community composition are lower than those in the topsoil (Li et al., 2021; Püschel et al., 2023). In addition, because of the abundance of plant litter on the surface, the soil nutrients on the soil surface are higher, which promotes the propagation of the microbial community (Bourget et al., 2023; Cheng et al., 2023). Microorganisms promote litter decomposition and allow plant-derived C to enter the soil C pool (Ridgeway et al., 2022).

## 5 Conclusions

Our study experimentally demonstrated that the soil physicochemical properties and enzyme activities of different plant communities in the proluvial fan in the eastern foothills of the Helan

Mountain were different due to community differences. The SOC content was ranked as *S. tianschanica* var. *gobica*>*E. rhgtidosperma*>*C. tragacanthoides*>*S. laricifolia*>*S. breviflora*. It was also observed that soil enzyme activities of ALP,  $\beta$ G,  $\beta$ X, and  $\beta$ D changed significantly at different soil depths. In addition, soil enzyme activities were closely related to the soil physicochemical properties in the study area and was affected by soil physicochemical properties to varying degrees, forming a complex network relationship. Here, we only investigated the changes in soil enzyme activities and two SOC fractions in different plant communities, whereas the mechanism of the formation and stabilization of SOC mediated by soil microorganisms in different plant communities was still unclear. In addition, studies on the formation and stabilization mechanisms of SOC in the study area are relatively limited, mainly because of the complexity of soil microbial communities and the multidimensional nature of SOC dynamics. Future studies should adopt comprehensive research methods combined with soil chemical analyses, microbial community structure and function analyses, and long-term positioning experiments to reveal the formation and stabilization mechanisms of SOC mediated by soil microorganisms in different plant communities. Stable isotope tracer techniques and molecular biology methods can be used to better understand the role of microorganisms in the SOC cycle and provide a scientific basis for soil C management.

## Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Author contributions

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